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DIETS OF YOUNG COLORADO SQUAWFISH AND OTHER SMALL FISH IN BACKWATERS OF THE GREEN RIVER, COLORADO AND UTAH

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ABSTRACT.—We compared diet of young-of-year Colorado squawfish (*Ptychocheilus lucius*), an endangered cyprinid, with diets of other fish <75 mm total length (TL) collected from backwaters of the Green River between river kilometers 555 and 35 during summer and autumn 1987. Species included native *Rhinichthys osculus*, *Catostomus discobolus*, and *C. latipinnis*, and nonnative *Cyprinella lutrensis*, *Notropis stramineus*, *Pimephales promelas*, *Ictalurus punctatus*, and *Lepomis cyanellus*. For each species, diet varied with size and between upper and lower river reaches but not between seasons for fish of similar size. Larval chironomids and ceratopogonids were principal foods of most fishes. Copepods and cladocerans were important in diets of *P. lucius* <21 mm TL and *L. cyanellus* <31 mm TL. *Catostomus discobolus* was the only species that ate moderate amounts of algae. Fish (all larvae) were in digestive tracts of only 10 *P. lucius* (21–73 mm TL), about 1% of *P. lucius* analyzed. High diet overlap occurred between some size-reach groups of *P. lucius* and *C. lutrensis*, *R. osculus*, *C. latipinnis*, *I. punctatus*, and *L. cyanellus*. Potential for food competition between young-of-year *P. lucius* and other fishes in backwaters appeared greatest with the very abundant *C. lutrensis*.

Key words: Ptychocheilus lucius, Cyprinella lutrensis, *nonnative fishes, young-of-year, diets, diet overlap, backwaters, Green River.*

Wild populations of federally endangered Colorado squawfish (*Ptychocheilus lucius*) persist only in the upper Colorado River basin. They are most abundant in the Green and Yampa rivers of eastern Utah and northwestern Colorado (Tyus 1991a). Decline of this and other native fishes in the Colorado River basin has been attributed to habitat alterations caused by water development and introduction and proliferation of nonnative fishes (Carlson and Muth 1989, Minckley 1991).

Backwaters of the Green River below its confluence with the Yampa River are important nursery areas for young-of-year (YOY) Colorado squawfish (Nesler et al. 1988, Haines and Tyus 1990, Tyus and Haines 1991). Ichthyofauna of these backwaters is dominated by nonnative fishes, especially red shiner (*Cyprinella lutrensis*; Tyus et al. 1982, Haines and Tyus 1990). This observation has led to a hypothesis that nonnative fishes adversely affect survival of young Colorado squawfish through competition or predation. Stanford (1993) suggested that strong food-web interactions between native and nonnative fishes probably occur, but dietary relationships have not been adequately documented (Haines and Tyus 1990, Ruppert et al. 1993). Our objectives

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were to (1) describe diets of YOY Colorado squawfish and other small fish in backwaters of the Green River and (2) examine diet overlap and potential for competition with Colorado squawfish.

METHODS

Samples of small fish were provided by the U.S. Fish and Wildlife Service Field Station at Vernal, UT. These were collected from backwaters of the Green River during summer (30 June–27 August) and autumn (22 September–10 December) 1987. The study area extends from confluence of the Green and Yampa rivers in Echo Park, Dinosaur National Monument, CO, to Turks Head in Canyonlands National Park, UT—river kilometer (RK) 555 to 35 above confluence with the Colorado River. Upper and lower reaches are divided at Sand Wash (RK 346), UT, a convenient access point just above Desolation Canyon. Each river reach began with a rocky, high-gradient (1.3–2.1 m/km) segment and continued with a sand- and silt-laden, low-gradient (0.2–0.4 m/km) segment known for relatively high catches of YOY Colorado squawfish (Haines and Tyus 1990, Tyus and Haines 1991). The river was further divided into 8-km sections starting from a random location within each reach to help assure an even distribution of collection sites.

Backwaters were defined as shallow (typically <0.5 m maximum depth), ephemeral embayments with negligible water velocity. Substrates consisted of silt and sand or silt and mud, sometimes overlaying or interspersed with gravel or cobble. Backwaters had little or no rooted aquatic vegetation, but some had dense mats of algae. Two backwaters were sampled weekly in each 8-km section during daylight (1000–1800 h) using 1-m^2 seines (0.8-mm^2 mesh) in summer and 1-m × 3-m seines (3.2-mm × 4.8-mm mesh) in autumn. Fish were killed and fixed in 10% formalin immediately after collection.

Up to five specimens ≤ 20 mm total length (TL) and five >20 mm TL of each fish species, representing graded size series, were selected from each sample. Each digestive tract (from esophagus to vent) was removed, opened, and visually assessed for percent fullness. Food items were identified to lowest practical taxon, and a visual estimate was made of percentage contributed by each taxon to total volume of food in each digestive tract (Larimore 1957, Mathur 1977). For diet analyses, food-item taxa (total of 124) were grouped into 20 family, order, or broader-based categories, sometimes divided according to habitat (e.g., aquatic or terrestrial).

Data for each fish species were stratified according to length (10-mm TL or larger intervals) by season (summer or autumn) within river reach (upper or lower). Only subsets with at least six fish containing food were included in analyses. Diet measures calculated for each subset were (1) mean percentage each food category contributed to total volume of food in each digestive tract (mean of volume percentages) and (2) percentage of all digestive tracts in which each food category occurred (percentage of occurrence). Wallace (1981) evaluated several diet measures and concluded that mean of volume percentages is the best measure for calculating overlap. However, percentage of occurrence is useful for describing general variations in diet (Wallace 1981, Bowen 1983).

Similarities in diet by subset between Colorado squawfish and other fishes were evaluated by Schoener's (1970) resource-overlap index:

$$\propto = 1 - 0.5\left(\sum_{i=1}^{n} |Pxi - Pyi|\right),$$

where n is the number of food categories, Pxi is the proportion of food category i (expressed as mean of volume percentages) in the diet of species x (Colorado squawfish), and Pyi is the proportion of food category i in the diet of species y (other fishes). Values range from 0.0 (no overlap) to 1.0 (complete overlap). When data on resource availability are absent, Schoener's index is one of the best indices available for calculating resource overlap (Hurlbert 1978, Linton et al. 1981, Wallace 1981). Diet overlap is useful in helping to elucidate food relationships among species and has been considered "biologically important" when values exceed 0.60 (Zaret and Rand 1971, Matthews and Hill 1980, Galat and Vucinich 1983).

RESULTS

Digestive tracts from 2554 fish representing 15 species were examined for food items;

<3% were empty, mostly from fish ≤ 13 mm TL. After subsets with <6 specimens containing food were eliminated from the data set, 2297 specimens representing nine species remained for diet analyses. Native fish included 972 Colorado squawfish (7.5–73.0 mm TL, mean = 19.1), 35 speckled dace (*Rhinichthys osculus*; 23.1–39.8 mm TL, mean = 28.1), 42 bluehead sucker (*Catostomus discobolus*; 23.0–58.9 mm TL, mean = 35.9), and 21 flannelmouth sucker (*C. latipinnis*; 32.0–64.3 mm TL, mean = 47.9). Nonnative fish included 729 red shiner (11.3–74.5 mm TL, mean = 29.1), 92 sand shiner (*Notropis stramineus*; 22.2–53.2 mm TL, mean = 31.0), 330 fathead minnow (*Pimephales promelas*; 11.0–65.9 mm TL, mean = 32.5), 58 channel catfish (*Ictalurus punctatus*; 22.5–70.0 mm TL, mean = 42.9), and 18 green sunfish (*Lepomis cyanellus*; 20.7–56.8 mm TL, mean = 39.6).

Characterization of Diets

No major or consistent seasonal differences in diet measures were observed within species for fish of similar size. Accordingly, summer and autumn data were combined for species and lengths by river reach. Trends in values of proportional importance of each food category were similar between the two diet measures for all fishes; therefore, only means of volume percentages are reported.

Diets consisted mostly of insects, zooplankton, algae, seeds, and organic and inorganic debris; but relative importance of these food categories varied among fishes or subsets within species (Table 1). Based on total number of food categories included in the diet of each fish species, diets of Colorado squawfish and red shiner were the most varied (18 and 17 food categories, respectively), followed by speckled dace (15), fathead minnow, channel catfish, and green sunfish (12 each), sand shiner (11), flannelmouth sucker (9), and bluehead sucker (6). Variety of food consumed was greater in the lower than upper reach for red shiner, Colorado squawfish, flannelmouth sucker, channel catfish, and green sunfish, whereas diets of sand shiner, fathead minnow, and speckled dace were more varied in the upper reach (diet of bluehead sucker was analyzed for fish from the upper reach only). Diet variety relative to fish length was greatest in red shiner, sand shiner, fathead minnow, Colorado squawfish, speckled dace, and bluehead sucker 21–30 or 31–40 mm TL and in flannelmouth sucker, channel catfish, and green sunfish >40 mm TL. Mean percent fullness of digestive tracts was highest in fish 21–30 or 31–40 mm TL for all species.

Aquatic insects were a principal part of diets for all fishes except fathead minnow and bluehead sucker. Of identifiable insects, immature dipterans (especially larval chironomids) were predominant in digestive tracts. Larval chironomids were represented by at least 21 genera, the most common being *Chironomus* followed by *Rheotanytarsus*, *Eukiefferiella*, *Polypedilum*, *Tanytarsus*, *Cricotopus*, and *Micropsectra*. Representative families of other immature dipterans were (in order of importance) Ceratopogonidae, Simuliidae, Dolichopodidae, Empididae, Muscidae, and Tipulidae. Proportional contribution of immature dipterans to diets of red shiner, sand shiner, speckled dace, and flannelmouth sucker was higher in the lower than upper reach. Relative importance of immature dipterans in diets of red shiner, sand shiner, and speckled dace decreased and utilization of other insects increased as fish length increased. Conversely, relative importance of immature dipterans in diets of Colorado squawfish and channel catfish increased or remained high with increasing fish length. Corixids, larval and adult aquatic coleopterans (predominantly Dytiscidae, Elmidae, Haliplidae, and Hydrophilidae), trichopteran larvae (mainly Hydropsychidae and Hydroptilidae), and ephemeropteran nymphs (predominantly Baetidae and Heptageniidae) were minor components of diets for all fishes (<10% of food volume) except larger red shiner, speckled dace, and green sunfish.

Red shiner and sand shiner ate more semiaquatic or terrestrial insects than other fishes. Semiaquatic insects consumed were primarily larval and adult coleopterans (predominantly Heterocercidae and Staphylinidae) and adult hymenopterans (Scelionidae). Terrestrial insects consumed were primarily hemipterans and formicids.

All fishes ate zooplankton, but it was particularly important in diets of Colorado squawfish <31 mm TL (especially <21 mm TL), green sunfish <31 mm TL, and, to a lesser extent, red shiner and channel catfish <31 mm TL and flannelmouth sucker. Cladocerans (many identified as *Daphnia*, *Eurycercus*, and *Macrothrix*) and especially cyclopoid copepods

TABLE 1. Diets by total-length intervals (mm) of nine fish species collected during summer and autumn 1987 from
sure is mean percentage contributed by each food category to total volume of food in each digestive tract (mean of vol-

Food category	Red shiner 11–20	Red shiner 21–30	Red shiner 31–40	Red shiner >40	Sand shiner 21–30	Sand shiner 31–40	Sand shiner >40	Fathead minnow 11–20	Fathead minnow 21–30	Fathead minnow 31–40	Fathead minnow >40	Colorado squawfish <11	Colorado squawfish 11–20
Upper reach[a]													
Insects													
Unidentifiable parts	11	9	25	37	3	9	22		2	1			1
Semiaquatic or terrestrial	1	4	6		12	5				<1			
Diptera immatures	30	27	29	13	25	19	3		7	4	4	13	70
Chironomidae adults	1	3	3	10	9	4	9						
Anisoptera nymphs													
Aquatic Coleoptera		3	10										
Corixidae		<1	1	10									
Trichoptera larvae	1	1	1									1	
Ephemeroptera nymphs		1					2						
Zooplankton													
Cladocera and Copepoda	7	6	3	3					<1	<1		26	16
Rotifera	6	<1							<1	<1	<1	16	1
Ostracoda						1			1				
Gammaridae													<1
Hydracarina												2	<1
Invertebrate eggs		1	1		<1	1				<1	<1	3	1
Nematoda	<1				1							6	1
Fish													
Plant seeds	7	9	<1	<1					1	1	4		<1
Algae	2	4	1		1	2			2	2	2	2	
Organic-inorganic debris	35	32	22	26	50	60	64		87	93	90	31	10
Number of fish	45	140	63	17	40	19	7	0	108	75	26	40	305
Mean % fullness of digestive tracts	52	64	44	38	81	77	73		83	84	75	40	59
Lower reach[a]													
Insects													
Unidentifiable parts	3	13	16	23	12	14	6		2	2	1		
Semiaquatic or terrestrial	9	8	10	11		2							<1
Diptera immatures	55	36	32	28	37	31	27	9	9	4	<1	19	47
Chironomidae adults	1	3	5	2									
Aquatic Coleoptera		2	1	3			6						
Corixidae			<1										
Trichoptera larvae		1	1	1								6	<1
Ephemeroptera nymphs	<1	1											
Anisoptera nymphs													
Zooplankton													
Cladocera and Copepoda	6	5	3	<1				1	1	<1	<1	29	35
Rotifera		<1	<1							<1		7	3
Ostracoda		<1	<1	<1			2		<1				
Gammaridae													
Hydracarina													
Invertebrate eggs	<1	1	<1			3						5	2
Nematoda		1	<1		9	18		1				1	1
Fish													
Plant seeds	9	7	4	5					<1		2		
Algae	1	1	1	1	2	<1		1	1	2	3		<1
Organic-inorganic debris	18	23	26	28	40	32	59	88	87	93	95	33	10
Number of fish	62	208	138	56	10	10	6	9	31	49	32	27	301
Mean % fullness of digestive tracts	58	60	49	36	66	52	37	72	85	80	78	45	70

[a]Upper reach = confluence of Green and Yampa rivers at RK 555 (river kilometers above confluence of the Green and Colorado rivers) in Echo Park, Dinosaur National Monument, CO, to Sand Wash, UT (RK 346); lower reach = Sand Wash to Turks Head, Canyonlands National Park, UT (RK 35).

backwaters in two reaches of the Green River below its confluence with the Yampa River, Colorado and Utah. Diet mea-
ume percentages).

Colorado squawfish			Speckled dace		Bluehead sucker			Flannelmouth sucker		Channel catfish			Green sunfish	
21–30	31–40	>40	21–30	31–40	21–30	31–40	>40	31–40	>40	21–30	31–40	>40	21–30	>40
Upper reach[a]														
10			34									4		
			2									1		
72	52	54	31		5	1		28	22			70		66
			8											
		8												13
	2		3											12
			4											2
		<1						8	13					1
1					1	<1								
									14					
2	6		5		<1	1								
	6											10		
	25	29												
			8		2	<1		<1						
					11	11	10		<1					
13	10	10	3		82	88	90	64	52			14		6
46	12	11	18	0	14	19	9	8	6	0	0	8	0	6
61	50	57	73		88	78	81	77	63			78		71
Lower reach[a]														
1	1		9	8						8	2	13		10
1	1									6	1	3		5
61	66	78	65	49					52	55	83	68	48	19
1	4											5	1	
<1				11								1		
														12
2	2		7	15								1		
				3										34
18	13	1	3						7	13	2		44	2
<1									<1					
									3					14
				5										
<1														
4														
1	2	6							<1	3		<1	<1	
<1	2	5												
1			8							3				
<1			<1						4	<1				
10	10	10	7	8					34	13	13	11	8	4
174	37	19	11	6	0	0	0	0	7	8	16	26	6	6
80	54	59	79	71					75	88	73	71	77	59

(many identified as *Cyclops*) represented most zooplankton found in digestive tracts. Identified genera of rotifers included *Brachionus*, *Cephalodella*, *Keratella*, *Lecane*, *Monostyla*, *Polyarthra*, and *Trichocerca*. Proportion of zooplankton in diets of all fishes tended to decrease with increasing fish length.

Bluehead sucker was the only species that ate moderate amounts of algae (10–30% of food volume); other fishes consumed minor amounts. Algae consisted mostly of six diatom genera (*Cymbella*, *Fragilaria*, *Gyrosigma*, *Navicula*, *Surirella*, and *Synedra*), one desmid genus (*Closterium*), and, to a lesser extent, *Pediastrum* (a colonial green alga). Most digestive tracts contained debris that accounted for moderate or large proportions of gut contents (>30%) in all fishes except speckled dace and green sunfish. It was over 80% of gut content in fathead minnow and bluehead sucker. Debris consisted of fibrous particles of vascular plant tissue usually mixed with large amounts of clay particles and sand grains, suggesting bottom feeding. Seeds (many identified as tamarisk [*Tamarix gallica*]) were eaten by all fishes, especially red shiner <31 mm TL.

Two observations were unique to Colorado squawfish. Fish larvae were found in digestive tracts of 10 Colorado squawfish (about 1% of total examined); 1 was 21 mm TL, 8 were 36–48 mm TL, and 1 was 73 mm TL (probably a yearling). No fish were detected in digestive tracts of other species. Of the 18 fish larvae found, most were too digested for species identification or accurate length measurement, but all were cypriniforms (mostly cyprinids) and probably ≤ 10 mm TL. Six fish larvae (6–9 mm TL) were identified as red shiner, and one (about 8 mm TL) as fathead minnow. Interestingly, the smallest Colorado squawfish had four prey fish (all red shiner), whereas only one or two fish were found in digestive tracts of the others. Gut contents of six Colorado squawfish, 36–48 mm TL, and the 73-mm-TL specimen were exclusively fish; those for the remaining specimens were 70–80% fish. Digestive tracts of six Colorado squawfish contained 2–6 cestode parasites (probably *Proteocephalus ptychocheilus*; Flagg 1982); cestodes were not found in guts of other fishes. Colorado squawfish infested with cestodes were larger than 27 mm TL and were collected from both river reaches in autumn.

Diet Overlap

Degree of diet overlap between YOY Colorado squawfish and other fishes was influenced mainly by zooplankton and especially immature dipterans (Table 2). Within each reach, diet overlap for all length intervals of Colorado squawfish generally decreased as lengths of other species increased. Degree of diet overlap among fish of similar size was generally greater in the lower than upper reach. Overlap values were <0.60 (range = 0.10–0.59) for most comparisons; generally, values were lowest for comparisons with fathead minnow and bluehead sucker (range = 0.10–0.44). Biologically important overlap (values >0.60) occurred only between Colorado squawfish >10 mm TL and some size-reach groups of native speckled dace and flannelmouth sucker and nonnative red shiner, green sunfish, and especially channel catfish. These higher overlap values were primarily attributed to high proportions of larval chironomids in diets and, secondarily, especially for diet overlap with green sunfish >40 mm TL (upper reach) and 21–30 mm TL (lower reach), to proportions of zooplankton. Degree of diet overlap was greatest with channel catfish and green sunfish.

DISCUSSION

Comparisons among food-habits investigations are difficult because of differences in study design, location, and season. However, our observations on diets of native and nonnative fishes in backwaters of the Green River generally agree with results of prior studies in the upper Colorado River basin (e.g., Vanicek and Kramer 1969, Jacobi and Jacobi 1982, McAda and Tyus 1984) and reported food habits of the nonnative species within their native ranges (e.g., Carlander 1969, 1977, Pflieger 1975, Harlan et al. 1987). Larger YOY or yearling red shiner, sand shiner, speckled dace, flannelmouth sucker, channel catfish, and green sunfish eat mainly immature aquatic insects. Diets of larger YOY or yearling fathead minnow and bluehead sucker consist mostly of algae and organic debris. Diet of YOY Colorado squawfish consists primarily of zooplankton and immature insects (especially chironomid larvae) and occasionally includes fish.

Reported size at which wild Colorado squawfish shift to a more piscivorous diet varies, but generally fish become an important food item after Colorado squawfish attain a length of >40 mm. Osmundson and Kaeding (1989) suggested that slower growth and poorer condition of YOY and especially yearling Colorado squawfish in grow-out ponds with lower densities of appropriate-size forage fish might have been caused by higher reliance on insect forage. Identifiable fish reported in digestive tracts of YOY Colorado squawfish here and by McAda and Tyus (1984) and Grabowski and Hiebert (1989) were either red shiner or fathead minnow larvae. These nonnative species are short-lived fractional spawners (Gale and Buynak 1982, Gale 1986) and are typically present in high numbers and at appropriate forage sizes in backwaters of the Green River throughout summer and autumn (Tyus et al. 1982, Karp and Tyus 1990). Karp and Tyus (1990) suggested that although the abundance of small nonnative prey fishes in the Green River might benefit growth of young Colorado squawfish, the benefit might be countered by the aggressive nature of some nonnative fishes, which could have negative effects on growth and survival of young Colorado squawfish. In their laboratory experiments on behavioral interactions, Karp and Tyus observed that red shiner, fathead minnow, and green sunfish shared activity schedules and space with Colorado squawfish and exhibited antagonistic behaviors toward smaller Colorado squawfish.

We could not effectively evaluate competition for food between YOY Colorado squawfish and other fishes because study design did not provide for estimation of resource abundance and availability, intraspecific diet selectivity, and effects of interspecific use of important resources. Direct evidence for interspecific competition should be determined through experiments demonstrating that shared use of a limited resource negatively affects one or more of the species (Schoener 1983, Underwood 1986, Wiens 1992). Additionally, we assume gut contents represented food consumed in the backwaters of capture, but this might not always have been the case. Tyus (1991b) observed that although young Colorado squawfish in the Green River were found mostly in backwaters, some moved to or from other habitats during 24-h periods. We found that diet overlap for most comparisons with Colorado squawfish was below the level generally considered biologically important (Table 2). Although not conclusive, these comparisons suggest either general resource partitioning or differences in diet preferences. Diet overlap values were considered biologically important only for comparisons with certain size-interval, river-reach groups of five fishes.

Because interspecific demand for resources might not exceed supply, Bowen (1983) noted that even extensive diet overlap is not conclusive evidence for competition. Accordingly, McAda and Tyus (1984), who also used Schoener's index to examine diet overlap between YOY Colorado squawfish and nonnative fishes in the Green River, suggested that high diet overlap they observed between Colorado squawfish 22–40 mm TL and channel catfish 19–55 mm TL (overlap value = 0.60) and especially red shiner 15–69 mm TL (overlap values 0.70–0.80) might reflect shared use of abundant resources, primarily immature dipterans, rather than competition. The same may be true for higher diet overlaps we observed. Ward et al. (1986) reported that chironomids, the principal food category resulting in high diet overlap, were among the more common benthic invertebrates in the Colorado River basin.

We observed that overlap values were generally higher and, for most fishes, diet variety was greater in the lower than upper reach, perhaps because food resources were more abundant and diverse in backwaters of the lower reach. Based on observations during summer and autumn 1979–1988, Haines and Tyus (1990) found that backwaters in the upper and lower reaches were similar in mean surface area, but that those in the lower reach were shallower and warmer, conditions that may favor higher productivity. Also, within the upper reach, Grabowski and Hiebert (1989) noted that during summer and autumn 1987–88 concentrations of backwater nutrients, particulate organic matter, phytoplankton, zooplankton, and benthic macroinvertebrates (particularly chironomid larvae) increased progressively downstream. They suggested this trend was due to attenuation of flow releases from Flaming Gorge Reservoir (located near the Wyoming-Utah border) at downstream sites that reduced the degree of water exchange between the main channel and backwaters and allowed for greater backwater warming and stability.

TABLE 2. Diet overlap by total-length (TL) intervals (mm) between young-of-year Colorado squawfish and eight other confluence with the Yampa River, Colorado and Utah. Overlap values were calculated using Schoener's (1970) index asterisk (*).

TL of Colorado squawfish	Red shiner								Sand shiner						Fathead minnow		
	Upper reach[a]				Lower reach[a]				Upper			Lower			Upper		
	11–20	21–30	31–40	>40	11–20	21–30	31–40	>40	21–30	31–40	>40	21–30	31–40	>40	21–30	31–40	>40
<11	0.59	0.54	0.40	0.43	0.42	0.49	0.50	0.47	0.46	0.47	0.35	0.53	0.55	0.52	0.40	0.37	0.38
11–20	0.49	0.45	0.43	0.31	0.63*	0.53	0.47	0.38	0.37	0.31	0.14	0.49	0.45	0.38	0.18	0.15	0.15
21–30	0.55	0.51	0.53	0.41	0.74*	0.57	0.51	0.42	0.42	0.43	0.27	0.49	0.47	0.38	0.23	0.19	0.23
31–40	0.40	0.39	0.40	0.27	0.73*	0.57	0.52	0.42	0.35	0.29	0.12	0.50	0.45	0.38	0.17	0.13	0.15
>40	0.39	0.37	0.39	0.35	0.65*	0.47	0.44	0.37	0.34	0.28	0.12	0.53	0.47	0.37	0.17	0.13	0.14

[a]Upper reach = confluence of Green and Yampa rivers at RK 555 (river kilometers above confluence of Green and Colorado rivers) in Echo Park, Dinosaur National Monument, CO, to Sand Wash, UT (RK 346); lower reach = Sand Wash to Turks Head, Canyonlands National Park, UT (RK 35)

Alternatively, greater diet overlap and variety in the lower reach might have been a reflection of a difference in backwater availability between the upper and lower reaches. Tyus and Haines (1991) reported about 150% more backwaters per kilometer in the upper than lower reach. Fishes in the lower reach might have been more crowded in available backwaters, resulting in greater shared use and broader intraspecific use of available food.

McAda and Tyus (1984) attributed reductions in diet overlap between Colorado squawfish >40 mm TL and red shiner or channel catfish to decreased consumption of immature dipterans and increased consumption of fish by Colorado squawfish. However, Ruppert et al. (1993) reported fish larvae in digestive tracts of 15% of adult red shiner (36–79 mm TL) from ephemeral shoreline embayments near confluence of the Green and Yampa rivers. Unlike our study, they sampled on a diel basis and killed fish with an overdose of anesthetic before preservation to minimize possible regurgitation. Their results suggest that high diet overlap between young Colorado squawfish ≥ 40 mm TL and red shiner might reoccur or continue with larger, piscivorous red shiner. Although we documented high diet overlap between young Colorado squawfish >10 mm TL and other fishes in backwaters of the Green River, especially channel catfish (Table 2), only red shiner, because of its extreme abundance (Haines and Tyus 1990), is likely to be a serious competitor for food with young Colorado squawfish. Red shiner has often been implicated in decline of native fishes of the American Southwest (e.g., Minckley 1973, Greger and Deacon 1988, Rinne 1991).

Competition might also be a factor between smaller specimens of both Colorado squawfish and other fishes. Few specimens <21 mm TL, other than red shiner and fathead minnow 11–20 mm TL, were available for comparisons with Colorado squawfish. However, as for smaller Colorado squawfish, zooplankton would likely be an important component of their diets (Joseph et al. 1977), and corresponding overlap values would be high, especially for specimens <11 mm TL. Although dense populations may develop in backwaters, zooplankton may be limited under certain conditions because plankton communities in rivers are subject to dramatic spatial or temporal fluctuations in abundance and diversity (Hynes 1970, Welcomme 1985, Ward 1989). In support of this generalization, Grabowski and Hiebert (1989) reported that zooplankton densities were higher in backwaters than in main-channel habitats within the upper reach and documented both spatial and temporal fluctuations in zooplankton abundance. They also observed higher concentrations of zooplankton in more confined backwaters than those with a broad connection to the river and suggested that densities were influenced by extent of water exchange between backwaters and the main river.

In conclusion, we found high diet overlap between YOY Colorado squawfish and several small size groups of other fish species in Green River backwaters. Because of the extreme abundance of red shiner, we speculate that diet overlap could result in food competition fish species collected during summer and autumn 1987 from backwaters in two reaches of the Green River below its with mean of volume percentages as the diet measure; values >0.60 (biologically important overlap) are marked with an

Fathead minnow				Speckled dace			Bluehead sucker			Flannelmouth sucker			Channel catfish				Green sunfish		
Lower				Upper	Lower		Upper			Upper		Lower	Upper	Lower			Upper	Lower	
11–20	21–30	31–40	>40	21–30	21–30	31–40	21–30	31–40	>40	31–40	>40	>40	>40	21–30	31–40	>40	>40	21–30	>40
0.44	0.43	0.37	0.33	0.21	0.36	0.34	0.39	0.35	0.34	0.52	0.57	0.59	0.34	0.46	0.34	0.30	0.21	0.56	0.25
0.22	0.21	0.15	0.11	0.37	0.59	0.57	0.16	0.12	0.11	0.46	0.45	0.65*	0.83*	0.72*	0.61*	0.57	0.73*	0.91*	0.26
0.21	0.21	0.15	0.12	0.52	0.76*	0.61*	0.20	0.16	0.19	0.42	0.36	0.69*	0.89*	0.81*	0.75*	0.75*	0.73*	0.75*	0.27
0.21	0.21	0.14	0.10	0.42	0.78*	0.61*	0.14	0.11	0.11	0.38	0.31	0.69*	0.68*	0.81*	0.79*	0.82*	0.61*	0.69*	0.27
0.21	0.20	0.14	0.10	0.35	0.74*	0.58	0.14	0.10	0.10	0.38	0.31	0.63*	0.64*	0.69*	0.89*	0.77*	0.68*	0.57	0.24

and might have a negative impact on Colorado squawfish growth, condition, or survival. Studies are needed to better assess the type and strength of interactions between native and nonnative fishes in backwater food webs under present regulated flow regimes and to define factors affecting these interactions.

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